

Primate Males

Causes and Consequences of Variation in Group Composition

The size and composition of primate groups vary tremendously across species, within species, and within groups over time. The most variable quantity is the number of adult males. In some groups, single males can monopolize access to several females, whereas reproduction is shared among several males in other groups. This variation lies at the heart of understanding adaptive variation among social systems. Whether groups contain single or multiple males has important consequences for the reproductive strategies of both sexes, and also shapes these animals' morphology and behavior.

Written by leading authorities, this book provides an extensive overview of variation in group composition across all major primate taxa, using up-to-date reviews, case studies, evolutionary theory and theoretical models, setting primates into context with birds and other mammals. It will become a firm favorite with all those interested in the behavioral ecology of primates.

PETER KAPPELER is Head of the Department of Behaviour and Ecology at the Deutsches Primatenzentrum in Göttingen, Germany. His research focuses on the lemurs of Madagascar, and he is co-editor of *Lemur Social Systems and their Ecological Basis* (1993) with J.U. Ganzhorn.



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Causes and Consequences of Variation in Group Composition

Edited by Peter M. Kappeler





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To Jakob and Josef - my dearest males



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Preface

This is a book about primate males. More specifically, its focus is on the causes and consequences of variation in the number of males per group within and across taxa. This variation lies at the heart of basic problems in primate socioecology, such as grouping patterns, reproductive strategies, social relationships, and dispersal.

Questions about the causes and consequences of variation in the number of males per group have a long history in studies of primate socioecology. In fact, they played a central role in the first systematic attempts to make sense out of the varied primate social systems and to understand their adaptive basis. Seminal papers by Crook & Gartlan, and Eisenberg and colleagues used the number of males as a variable to organize the rapidly growing information about primate social systems. The resulting categories were used to examine correlations with ecological variables, an approach that had been successfully applied earlier to birds.

Subsequent studies by Clutton-Brock, Harvey and others used the distinction between single-male and multimale species to explain successfully variation in other traits, but there were no breakthroughs on the question of the adaptive origins of the social systems *per se*. Despite, or perhaps because of, growing dissatisfaction with these largely correlational studies, most researchers moved on to other questions, and, as Harvey & Harcourt put it retrospectively in 1984, 'the question of single-male versus multimale breeding systems remained a matter of speculation'.

Following important papers by Wrangham and van Schaik, the focus began to shift toward questions about female behavior in the early 1980s, perhaps also because females were practically ignored in the first classificatory approaches. Important papers by Ridley, Andelman, Wrangham, and Jeanne Altmann revisited the issue in the late 1980s, but it was not until recently that new questions, methods, and data generated renewed interest in primate males and their behavior. Most recently, carefully controlled comparative studies re-examined potential determinants of the number of males in primate groups, albeit with somewhat conflicting conclusions.

We were therefore confronted with a situation characterized by partly unresolved old, fundamental questions, a wealth of data on the diversity of primate social systems from many new field studies, as well as important theoretical and methodological advances. Time was therefore ripe for a basic inventory and some organizing questions. An international conference with focused contributions by the recognized authorities on various taxa and topics seemed to be an appropriate way to assess and organize the existing information. This conference took place in December 1997, hosted by the German Primate Center (DPZ). For four days, 19 invited speakers and more than 200 other participants discussed 47 oral and poster presentations. Following the conference, 21 contributions were submitted in written form, and each one was subjected to rigorous peer review. These contributions constitute a representative sample of the contributions to the conference, encompassing specific case studies, comprehensive reviews, theoretical modeling, as well as studies of non-primate societies that provide important comparative perspectives on general principles.

The conference, as well as the resulting volume, would not have been possible without the help of many people and organizations. The first Göttinger Freilandtage were made possible by generous grants from the Deutsche Forschungsgemeinschaft (DFG), the Wenner-Gren Foundation for Anthropological Research, the Niedersächsisches Ministerium für Wissenschaft und Kultur, and the Sparkasse Göttingen. Michael Lankeit generated the idea of the Göttinger Freilandtage and subsequently supported their first installment in many ways. All members of the Abteilung Verhaltensforschung/Ökologie of the DPZ, in particular Andreas Koenig, Carola Borries, Dietmar Zinner, Eckhard Heymann, Christoph Knogge, Stephanie Heiduck, Julia Ostner, Oliver Schülke, and Ulrike Walbaum helped beyond the call of duty with logistical and organizational problems. Other members of the DPZ, especially Rudi Ilse, Erhard Neuhaus, Michael Schwibbe, and Silke Singer provided much appreciated help with various practical problems. Tracey Sanderson's advice and encouragement



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were crucial in realizing this volume. Ulrike Walbaum had the nerves to compile the joint reference list, and Carel van Schaik, Volker Sommer and Michael Pereira provided helpful suggestions about the organization of this book. I thank all of them. This book is dedicated to my father

and son, who, like the rest of my family, supported and inspired me in many ways during the evolution of this volume.

Göttingen, January 1999

Peter M. Kappeler